

THE PYCNOGONID GENUS RHOPALORHYNCHUS

WOOD-MASON, 1873

BY

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INTRODUCTION

One of the most difficult families of Pycnogonida is that of the Colossendeidae. Diverse problems seem to converge in this family: the presence of several extra-legged genera; the critical delimitation of genera and species; the considerable variation of specific characters; the abundance of very wide, even world-wide, distributed deep sea species; the obscurity of secondary sexual characters; the lack of data on the reproduction.

Observations on reproduction are lacking in two pycnogonid families only, the Austrodecidae and the Colossendeidae. Since such observations are abundant with regard to other pycnogonid families, it is tempting to assume an aberrant reproduction in the two families just mentioned. The Austrodecidae were the subject of an exhaustive account in a recent paper (STOCK, 1957c). In that family, the taxonomic relations between the species form a strong support for the assumption of an aberrant reproduction.

In order to complete our ideas on the mode of speciation in the Pycnogonida, I started a revision of the second family, the Colossendeidae, in which an abnormal reproduction was suspected. It soon became clear, that a revision of the entire family, with its many deep sea species, known from very few specimens, did not belong to the possibilities at this moment. Therefore, I confined myself to some revisionary work on the only shallow water genus of the family, *Rhopalorhynchus*. The present paper gives a taxonomic revision of the genus, a redescription of most of its species, and a discussion on the mode of speciation. In general, the results are very similar to those obtained in my revision of the Austrodecidae (STOCK, 1957c), viz., that speciation through geographic isolation is of outstanding importance in marine organisms as Pycnogonida.

COLOSSENDEIDAE

The genus *Rhopalorhynchus* belongs to the family Colossendeidae. This family, in the sense adopted by most British and American authors (CALMAN, GORDON, HEDGPETH), seems to be a quite natural group. The family can be diagnosed as follows:

Four to six trunk segments, four to six pairs of legs. Proboscis very well developed, not annulated. Chelifores in various degrees of reduction: often completely absent or deciduous, sometimes persistent in adults, but in the latter case

Table 1. Survey of the synonymy in the genus *Rhopalorbynchus*

author, year	old name	new name
WOOD-MASON, 1873	<i>Rhopalorbynchus Kröyeri</i>	<i>Rh. kroeyeri</i>
HASWELL, 1885	<i>Colossendeis tenuissima</i>	<i>Rh. tenuissimum</i>
CARPENTER, 1893	<i>Rhopalorbynchus clavipes</i>	<i>Rh. clavipes</i>
CARPENTER, 1907	<i>Rhopalorbynchus gracillimus</i>	<i>Rh. gracillimum</i>
		<i>Rh. lomani</i>
		<i>Rh. lomani</i>
LOMAN, 1908	<i>Rhopalorbynchus kröyeri</i>	<i>Rh. sibogae</i>
		<i>Rh. gracillimum</i>
	<i>Colossendeis articulata</i>	<i>Rh. articulatum</i>
LOMAN, 1911	<i>Colossendeis dofleini</i>	<i>Rh. dofleini</i>
FLYNN, 1911	<i>Rhopalorbynchus tenuissimus</i>	<i>Rh. tenuissimum</i>
		<i>Rh. kroeyeri</i>
CALMAN, 1923	<i>Rhopalorbynchus kröyeri</i>	<i>Rh. ? clavipes</i>
		<i>Rh. lomani</i>
		<i>Rh. gracillimum</i>
OHSHIMA, 1936	<i>Colossendeis dofleini</i>	<i>Rh. dofleini</i>
CALMAN, 1938	<i>Rhopalorbynchus kröyeri</i>	<i>Rh. lomani</i>
HEDGPETH, 1939	<i>Colossendeis californica</i>	<i>Rh. californicum</i>
HEDGPETH, 1941	<i>Colossendeis californica</i>	<i>Rh. californicum</i>
	<i>Colossendeis chitinososa</i>	<i>Rh. chitinosum</i>
HILTON, 1943	<i>Colossendeis californica</i>	<i>Rh. californicum</i>
	<i>Colossendeis dofleini</i>	<i>Rh. dofleini</i>
HEDGPETH, 1949	<i>Colossendeis chitinososa</i>	<i>Rh. chitinosum</i>
UTINOMI, 1951	<i>Colossendeis dofleini</i>	<i>Rh. dofleini</i>
		<i>Rh. kroeyeri</i>
		<i>Rh. gracillimum</i>
		<i>Rh. lomani</i>
STOCK, 1953	<i>Rhopalorbynchus kröyeri</i>	<i>Rh. sibogae</i>
		<i>Rh. tenuissimum</i>
		<i>Rh. clavipes</i>
		<i>Rh. kroeyeri</i>
STOCK, 1954	<i>Rhopalorbynchus kröyeri</i>	<i>Rh. mortenseni</i>
		<i>Rh. gracillimum</i>
BARNARD, 1954	<i>Rhopalorbynchus kröyeri</i>	<i>Rh. dofleini</i>
	<i>Colossendeis dofleini</i>	<i>Rh. dofleini</i>
UTINOMI, 1955	<i>Colossendeis chitinososa</i>	<i>Rh. chitinosum</i>
STOCK, 1957a	<i>Rhopalorbynchus pedunculatum</i>	<i>Rh. pedunculatum</i>
STOCK, 1957b	<i>Rhopalorbynchus kroeyeri</i>	<i>Rh. kroeyeri</i>

always shorter than the proboscis, with gaping, smooth fingered, chelae. Palpi well-developed, 8- to 10-segmented. Ovigera equally well developed in both sexes, with several rows of special spines on the terminal four segments. Oviger segments 4 and 6 elongated, segment 5 short. Ovigerous specimens unknown (unless the adherent bodies or capsules occasionally found attached to the legs are egg capsules).

Hitherto, the family was defined by the structure of chelifores and palps, but in my opinion stress should also be laid on the oviger structure.

The six genera belonging to the family Colossendeidae can be determined as follows:

- 1a) Four pairs of legs 3
- b) Five pairs of legs 2
- c) Six pairs of legs *Dodecolopoda* Calman & Gordon, 1933
- 2a) Chelifores present in adults *Decolopoda* Eights, 1835 *)
- b) Chelifores absent in adults *Pentacolossendeis* Hedgpeth, 1943
- 3a) Trunk segments (usually) fused. Abdomen well-developed. Coxae 1 to 3 subequal. Lateral processes not widely separated. *Colossendeis* Jarzinsky, 1870
- b) Trunk segments free. Abdomen minute. Coxae 1 to 3 subequal. Lateral processes widely separated *Rhopalorhynchus* Wood-Mason, 1873
- c) Trunk segments free. Abdomen well-developed. Coxa 2 longer than coxa 1 or 3. Lateral processes widely separated *Pipetta* Loman, 1904

Rhopalorhynchus

The genus *Rhopalorhynchus* may be diagnosed in the following way:

Very slender animals, with 4 free trunk segments and widely separated lateral processes. Abdomen minute, more or less ventral in position. Proboscis spindle-shaped, with a narrow, usually more or less stalk-like, basal part. Chelifores absent. Palps 10-segmented. Ovigera 10-segmented, with terminal claw that, together with a spine on the 10th oviger segment, forms a kind of subchelate structure. Genital pores (♀, ♂) on the ventral surface on coxae of all legs. No auxiliary claws.

In this diagnosis, emphasis has been laid on the segmentation of the trunk, the reduction of the abdomen, and — although in a lesser degree — on the shape of the proboscis, the subchelate oviger, and the slenderness of the trunk. These characters are, in my opinion, important enough to warrant generic separation of *Rhopalorhynchus* from other genera, more particularly from *Colossendeis*. In the past, wittingly or unwittingly the only character used for the differentiation of *Rhopalorhynchus* and *Colossendeis* was the presence or absence of a spine-like protuberance on the dorsal surface of the proboscis. In the emended sense, the genus *Rhopalorhynchus* has a more solid base. This base is not only morphological, but also ecological: the members of *Colossendeis* are inhabitants of deep water, the members of *Rhopalorhynchus* are inhabitants of shallow water (recorded from 0 to 924 m; one species only lives in the deep sea, 1944 m). The genus *Rhopalorhynchus*, in its new conception, will contain the species that were previously already referred to that genus, but in addition likewise some species formerly attributed to *Colossendeis*:

*) As to the date of publication, see CALMAN, 1937, p. 182.

Rb. kroeyeri Wood-Mason, 1873
 (genotype)
Rb. tenuissimum (Haswell, 1885)
Rb. clavipes Carpenter, 1893
Rb. gracillimum Carpenter, 1907
Rb. articulatum (Loman, 1908)

Rb. dofleini (Loman, 1911)
Rb. californicum (Hedgpeth, 1939)
Rb. chitinosum (Hilton, 1943)
Rb. lomani spec. nov.
Rb. sibogae spec. nov.
Rb. pedunculatum Stock, 1957a
Rb. mortenseni spec. nov.

VARIABILITY, SECONDARY SEXUAL DIFFERENCES

The variability is considerable in this genus. Especially in the shape of the proboscis and of the eye tubercle, an unlimited amount of possibilities seems to be present. In order to fix to a certain extend the differences in shape of the proboscis, I have taken 6 standard measurements from many specimens, which I called α , β , γ , δ , ϵ , and ζ (fig. 1).

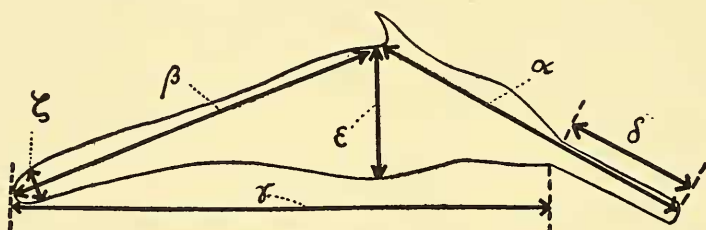


Fig. 1. The six standard measurements of the proboscis. α : the place of the tooth, β : the length of the produced part, γ : the length of the inflated part, δ : the length of the stalk, ϵ : the diameter of the inflated part, ζ : the diameter of the produced part.

In general the following facts are clear:

- (1) In female the inflated part of the proboscis (γ) is longer than in male.
- (2) The stalk of the proboscis (δ) is in female relatively shorter than in male.
- (3) The place of the tooth is remarkably constant in both sexes and in material from different localities.
- (4) The absolute size of specimens attributed to the same species varies considerably.
- (5) The inflation of the femur in female varies considerably, probably in relation to the degree of maturity and the reproductive season.
- (6) The length of tarsus, propodus, and claw varies from leg to leg. Usually, the absolute size of these joints is the smallest on leg 1, the largest on leg 3. In relative size, the claw is the longest on legs 3 and 4.

With some experience the sexes can be determined by the shape and relative proportions of the proboscis (cf. 1, and 2 in the above list) but the most reliable characters for the determination of the sex are the size and position of the genital pores. The male genital pores are small, situated on the ventro-distal surface of the second coxa. In female the genital pores are large, situated on $1/2$ to $2/3$ of the second coxa. In fully mature material the inflation of the distal part of the femoral joints in female is easily discernible. There is no difference in length of the claws in the two sexes, contrary to the supposition of BARNARD, 1954, p. 89.

KEY TO THE SPECIES

The taxonomy of the genus *Rhopalorbynchus* runs completely parallel with that of the closely related genus *Colossendeis*. The characters used for separating the species are the same in both genera: the shape of the proboscis, the ratio between tibia 2 and tarsus + propodus + claw, the relative length of palp segment 6. In analogy with *Colossendeis* the genus is subdivided in a longitarsal and a brevitarsal group.

I. Proboscis with a tooth in the middle of the inflated part.

Rb. kroeyeri Wood-Mason

II. Proboscis with a tooth before the middle of the inflated part.

A. Longitarsal species (in the third leg the tarsal ratio

$\frac{\text{tarsus} + \text{propodus} + \text{claw}}{\text{tibia } 2} = 70\text{--}100\%$). Claw $1/2$ to 1 times as long as the propodus.

a. Tarsal ratio 70—90%. Eye tubercle conical, pointed. Palp segment 6 $2/3$ to 1 times as long as segment 7. Proboscis acuminate, distal part narrowly produced. Claw half as long, or slightly more than half as long, as the propodus. *Rb. lomani* spec. nov.

b. Tarsal ratio 85—100%. Eye tubercle rounded, obtuse. Palp segment 6 $1/2$ to $2/3$ of segment 7. Proboscis not narrowed, cylindrical to spindle-shaped. Claw nearly as long as the propodus. *Rb. sibogae* spec. nov.

c. Characters uncertain (published descriptions inadequate).

Rb. tenuissimum (Haswell)

B. Brevitarsal species (in the third leg the tarsal ratio

$\frac{\text{tarsus} + \text{propodus} + \text{claw}}{\text{tibia } 2} = 45\text{--}70\%$). Claw at most half as long as the propodus.

a. Stalk of the proboscis longer than the inflated part ($\delta > \gamma$). Palp segment 6 $1/2$ to $2/3$ of segment 7. *Rb. pedunculatum* Stock

b. Stalk of the proboscis shorter than the inflated part ($\delta < \gamma$). Palp segment 6 $2/3$ to 1 times as long as segment 7.

1. Proboscis regularly spindle-shaped. Eye tubercle conical. Tarsus and propodus scantily setose. Palp segments 7 to 10 rather short. Tarsal ratio 67%. Tooth situated at 37% of the length of the inflated part of the proboscis. *Rb. clavipes* Carpenter

2. Proboscis acuminate, distal part narrowly produced, bent downward. Eye tubercle highly conical. Tarsus and propodus densely setose. Palp segments 7 to 10 rather short. Tarsal ratio 50—65%. Tooth situated at 18—27% of the length of the inflated part of the proboscis. *Rb. gracillimum* Carpenter

3. Proboscis intermediate between *clavipes* and *gracillimum*. Eye tubercle intermediate between *clavipes* and *gracillimum*. Tarsus and propodus densely setose. Palp segments 7 to 10 slender. Tarsal ratio 46%. Tooth situated at 34—35% of the proboscis

Rb. mortenseni spec. nov.

III. Proboscis without tooth.

Rb. articulatum (Loman), *Rb. dofleini* (Loman), *Rb. californicum* (Hedgpeth), *Rb. chitinosum* (Hilton). These species, formerly attributed to *Colossendeis*, will not be treated in this paper.

DESCRIPTIONS OF THE SPECIES

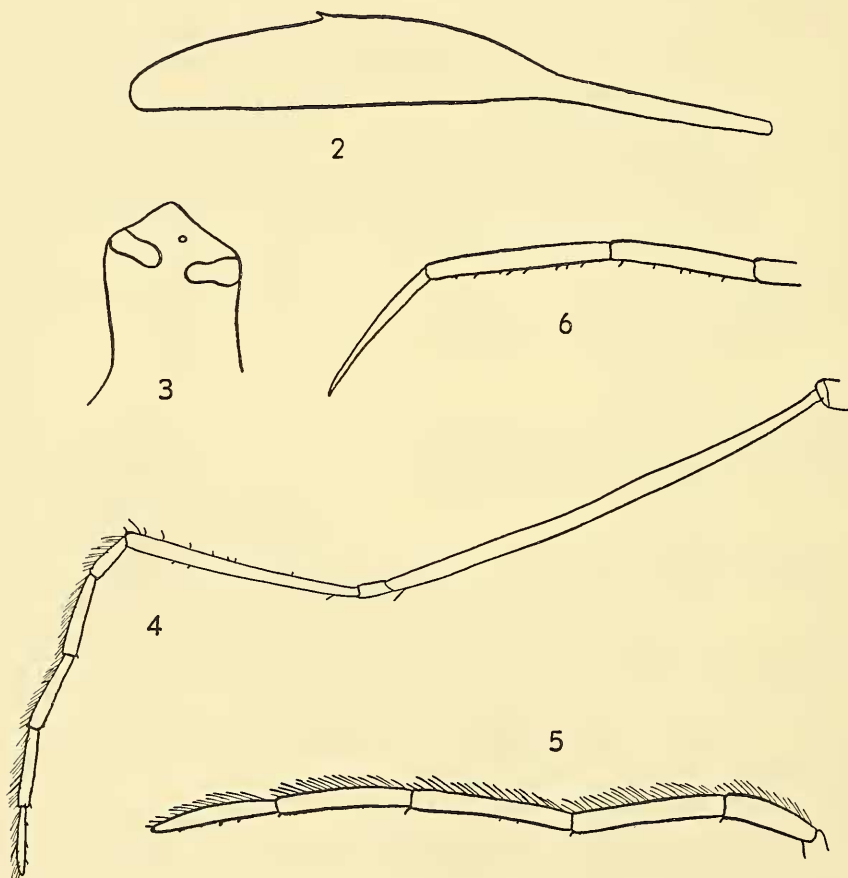
***Rhopalorhynchus kroeyeri* Wood-Mason. Figs. 2—6.**

Rb. Kröyeri Wood-Mason, 1873 (8 Nov.), pp. 172—175, pl. XIII, figs. 1—5.

Rb. kröyeri, Calman, 1923 (part., only the Andaman record), pp. 268—270, fig. 1 (re-illustration of the type).

Rb. kröyeri, Stock, 1954 (part., only the Kei Is. record), pp. 161—162.

Rb. kroeyeri, Stock, 1957b, p. 97.



Figs. 2—6. *Rhopalorhynchus kroeyeri* Wd.-Mason, ♀, from the Philippine Islands. 2, Proboscis; 3, eye tubercle from left-hand side; 4, palp; 5, distal segments of palp; 6, distal segments of second leg

Type specimen: ♂. Indian Museum, Calcutta. Reg. no. 401.

Material examined: 2 females. Philippine Islands. Zool. Mus. Hamburg, cat. no. 17622. — 1 male. Danish Expedition to the Kei Islands, Stat. 38. N.E. of Doe Roa. Trawl. About 35 m. Sand. Apr. 24, 1922. Collected by Dr. Th. MORTENSEN. Zool. Mus. Copenhagen.

Distribution: East Indian Archipelago (Port Blair, Andaman Islands — type locality —; Philippines; Kei Islands).

Bathymetrical range: 35—46 m.

Diagnostic features: The inflated part of the proboscis is sausage-shaped, with a small tooth in the middle of the inflated part (in the studied specimens on 49%, 54% and 54% of the length). Eye tubercle lowly conical above the eyes. Palp segment 6 relatively short, segments 7 to 10 slender. Legs longitarsal (tarsal ratio of 3rd leg 76%, 85%, 88%). Claw very long, $\frac{2}{3}$ to 1 times as long as the propodus. Propodus and tarsus scantily setose at the inner margin. Tarsus shorter than the propodus.

Measurements in mm of a male from the Kei Islands, and of two females from the Philippines, respectively :

Trunk, segment 1: ♂ 0.60, ♀ 0.83, ♀ —; segment 2: 2.00, 2.13, —; segment 3: 1.87, 2.07, —; segment 4: 0.93, 1.20, —.

Width across the 2nd lateral processes: 1.07, 1.33, —.

Proboscis α 3.60, 4.40, 4.20; β 1.20, 1.80, 1.80; γ 2.60, 3.73, 3.53; δ 2.13, 2.07, 2.33; ϵ 0.60, 0.73, 0.70; ζ 0.30, 0.40, 0.40.

Third leg, femur 6.20, 7.93, —; tibia 1 5.40, 7.33, —; tibia 2 4.07, 5.67, —; tarsus 1.00, 1.27, —; propodus 1.40, 1.60, —; claw 1.17, 1.33, —.

Rhopalorhynchus lomani spec. nov. (Figs. 7—21)

Rb. gracillimus, Carpenter, 1907 (part., only the Saya de Malha record), p. 100.

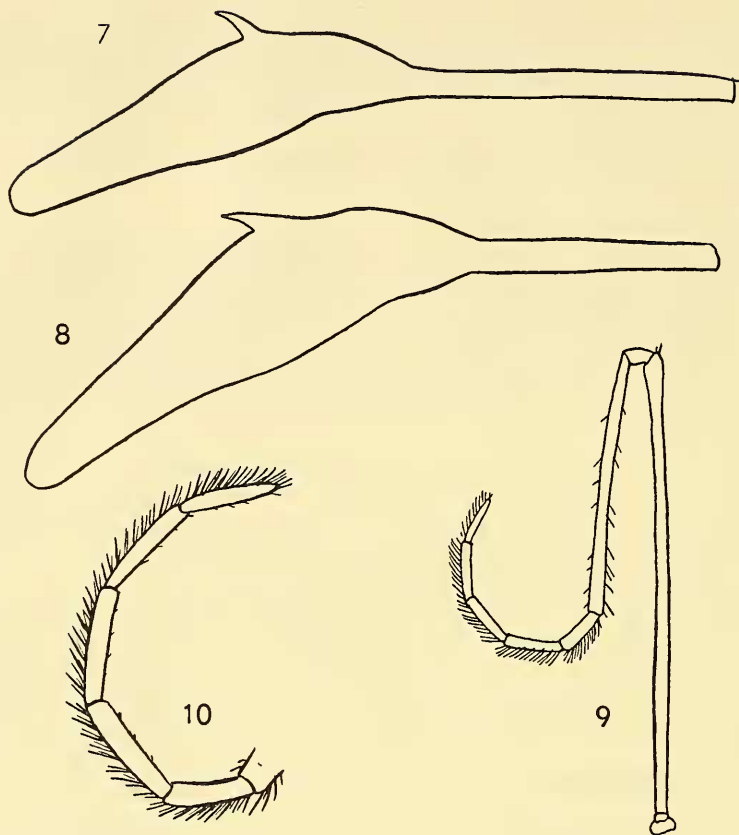
Rb. kröyeri, Loman, 1908 (part., only Siboga Stats. 184, 213, and part of the material of Stat. 50), pp. 24—27, pl. XV, figs. 213—215, 219.

Rb. kröyeri, Calman, 1923 (part.), pp. 268—270.

Rb. kröyeri, Calman, 1938, p. 149.

Type specimens: 1 ♂ (holotype) and 1 ♀ (allotype) from Siboga, Stat. 50. Zool. Mus. Amsterdam, cat. no. Pa. 1308.

Material examined: 22 females, 16 males. Siboga Stat. 50. Labuan Badjo, West coast of Flores. 27—36 m. Mud and sand. Zool. Mus. Amsterdam Pa. 1309. — 1 male. Siboga Stat. 184. Manipa Island, between Ceram and Buru. 36 m. Sand. Zool. Mus. Amsterdam Pa. 1313. — 1 male. Siboga Stat. 213. Near Saleyer. 45 m. Sandy mud. Zool. Mus. Amsterdam Pa. 1314. — 2 females, 3 males. Between Masqat (= Mascat, = Maskat) and Mutha Harbors, Gulf of Oman. Brit. Mus. (Nat. Hist.), reg. no. 1914.7.21. 6—10. — 1 female. John Murray Exp. Stat. M.B. II C. Arabian coast. 29 m. Oct. 28, 1933, Brit. Mus. (Nat. Hist.). — 4 females, 2 males. John Murray Exp. Stat. M.B., B. Red Sea. 29 m. Sep. 17, 1933. Brit. Mus. (Nat. Hist.). — 53 specimens. John Murray Exp. Stat. M.B., D. Red Sea. 26 m. Sep. 17, 1933, Brit. Mus. (Nat. Hist.). — 1 male. Percy Sladen Trust Exp. Stat. C 12. Saya de Malha. 86 m. (Syntype of *Rb. gracillimum* Carpenter). Brit. Mus. (Nat. Hist.).



Figs. 7—10. *Rbopalorbynchus lomani* spec. nov., from Siboga Stat. 50. 7, Proboscis of ♂; 8, proboscis of ♀; 9, palp of ♂; 10, distal segments of palp of ♀.

Distribution: East Indian Archipelago, Red Sea, Arabian coast, Saya de Malha. Bathymetrical range: 26—86 m.

Diagnostic characters: The inflated part of the proboscis is narrowly produced, with a strong tooth on 32—38% of the length. Eye tubercle with a strongly conical apical point. Palp segment 6 relatively well-developed, $\frac{2}{3}$ to 1 times as long as segment 7. Segments 7 to 10 not very slender. Legs longitarsal (tarsal ratio of 3rd leg in 12 specimens 72%, 74%, 77%, 78%, 78%, 78%, 79%, 79%, 79%, 87%, 87%). Claw on the first leg half the length of the propodus, or slightly less; on the 3rd and 4th legs distinctly more than half the propodus. Tarsus and propodus fairly setose at the inner margin.

Measurements of specimens from the type locality, Siboga Stat. 50 (in mm).

Trunk, segment 1 ♂ 0.90, ♀ 1.00; segment 2 ♂ 2.40, ♀ 2.00; segment 3 ♂ 2.53, ♀ 2.07, segment 4 ♂ 0.87, ♀ 0.67.

Width, across the 2nd lateral processes ♂ 1.27, ♀ 1.33.

Proboscis of male α 3.47, 3.17, 3.67, 3.73, 4.20; β 2.20, 1.93, 2.13, 1.93, 2.33;

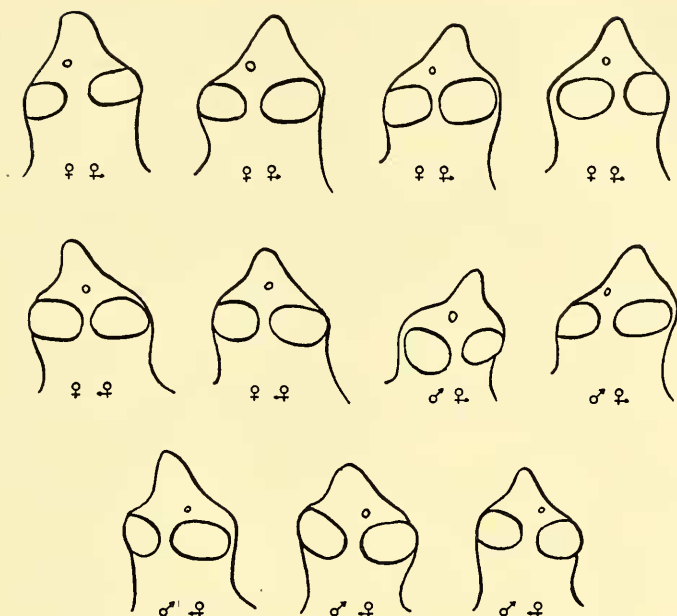


Fig. 11. *Rhopalorbynchus lomani* spec. nov., from Siboga Stat. 50. Various types of eye tubercles, in side view

γ 3.20, 2.90, 3.33, 2.93, 3.53; δ 2.00, 1.87, 2.27, 2.40, 2.73; ϵ 0.87, 0.77, 0.83, 0.80, 0.87; ζ 0.33, 0.30, 0.33, 0.33, 0.40.

Proboscis of female α 4.13, 4.13, 4.07, 3.67, 3.73; β 2.80, 2.87, 2.80, 2.53, 2.77; γ 4.53, 4.40, 4.20, 3.67, 4.20; δ 2.33, 2.20, 2.20, 2.00, 1.87; ϵ 1.03, 1.07, 1.00, 0.97, 1.03; ζ 0.43, 0.40, 0.40, 0.33, 0.47.

First leg of male (tarsus, propodus, claw, respectively) 2.40, 2.00, 1.13; First leg of female 2.07, 1.83, 0.90; Fourth leg of male 2.20, 2.13, 1.40; Fourth leg of female 2.07, 2.00, 1.13.

Third leg, femur δ 7.6, γ 7.6; tibia 1 δ 7.6, γ 6.9; tibia 2 δ 7.2, γ 6.6.

Measurements of specimens from JOHN MURRAY Exp., St. M.B., D.

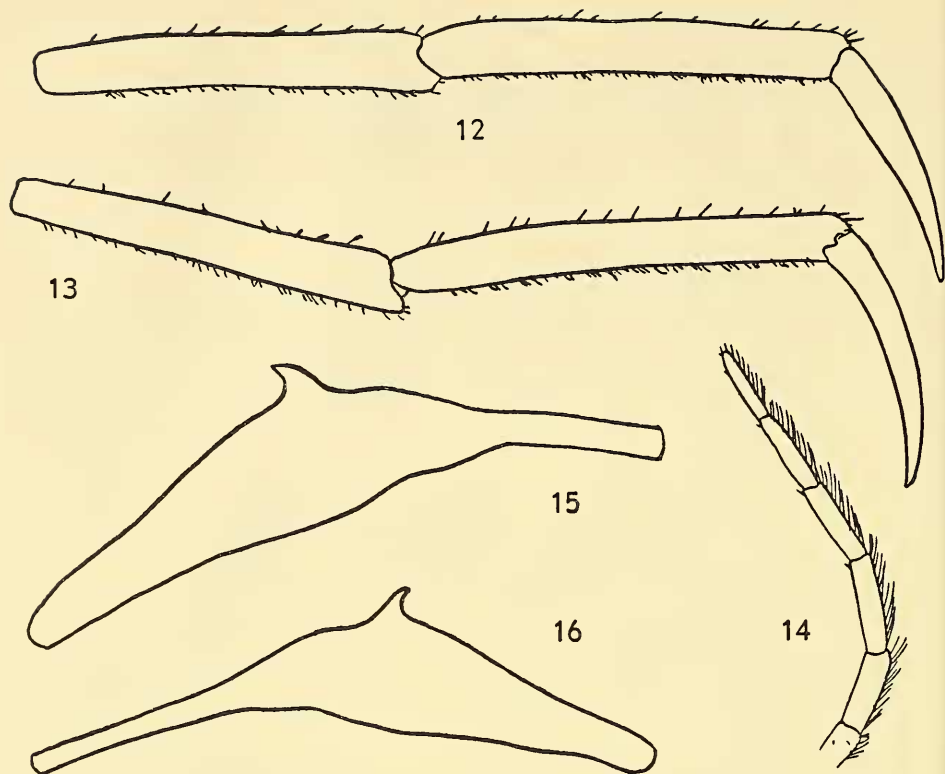
Trunk, segment 1 (δ and γ , respectively) 1.00, 1.13; segment 2 2.07, 2.40; segment 3 2.00, 2.20; segment 4 0.93, 0.93.

Width, across the 2nd lateral processes δ 2.07, γ 2.87.

Proboscis of male α 3.53, 3.33, 3.93, 3.73, 3.20; β 2.53, 2.20, 2.47, 2.73, 2.40; γ 3.80, 3.53, 3.67, 3.87, 3.33; δ 1.87, 1.87, 3.20, 2.37, 2.73; ϵ 0.90, 0.87, 0.90, 0.83, 0.83; ζ 0.33, 0.30, 0.37, 0.30, 0.30.

Proboscis of female α 3.57, 3.47, 3.47, 3.77, 4.20; β 3.13, 3.40, 3.33, 3.20, 3.00; γ 4.60, 4.93, 4.67, 4.53, 4.67; δ 1.67, 1.67, 2.20, 1.93, 2.07; ϵ 1.13, 1.13, 1.07, 0.93, 1.17; ζ 0.40, 0.43, 0.43, 0.30, 0.47.

First leg of male (tarsus, propodus, claw, respectively) 1.53, 1.73, 0.87; First leg of female 1.60, 1.90, 0.90; Fourth leg of male 1.60, 1.93, 1.07; Fourth leg of female 1.67, 2.07, 1.17.



Figs. 12—16. *Rhopalorbynchus lomani* spec. nov., from John Murray Exp. Stat. M.B., D. (Red Sea). 12, distal segments of first leg of ♂; 13, distal segments of fourth leg of ♂; 14, distal palp segments of ♀; 15, proboscis of ♀; 16, proboscis of ♂

Third leg, femur (♂ and ♀, respectively) 6.5, 7.6; tibia 1 6.8, 7.1; tibia 2 5.9, 6.2.

Measurements of 2 males, from Siboga, Stat. 184 and 213, respectively.

Proboscis α 3.67, 3.93; β 1.87, 1.67; γ 3.00, 2.73; δ 2.33, 2.60; ε 0.73, 0.77; ζ 0.33, 0.30.

Tarsus P 1, 2.07, —; P 2, —, 2.07; P 3, 2.13, 2.07; P 4, 2.00, 2.07; Propodus, P 1, 1.67, —; P 2, —, 1.80; P 3, 1.73, 1.80; P 4, 1.73, 1.93; Claw, P 1, 0.77, —; P 2, —, 1.00; P 3, 0.93, 1.13; P 4, 0.97, 1.20; Femur, P 3, 7.2, 7.1; Tibia 1, P 3, 7.0, 7.0; Tibia 2, P 3, 6.5, 6.5.

Measurements of a female from JOHN MURRAY Exp. Stat. M.B. IIC, and of a male from Percy Sladen Trust Exp., Stat. C 12., respectively.

Trunk, segment 1 0.80, —; segment 2 2.13, —; segment 3 1.93, —; segment 4 0.73, —.

Width across the 2nd lateral processes 1.53, —.

Proboscis α 2.80, 3.47; β 1.63, 3.20; γ 2.40, 4.87; δ 1.80, 1.33; ε 0.73, 1.20; ζ 0.33, 0.40.

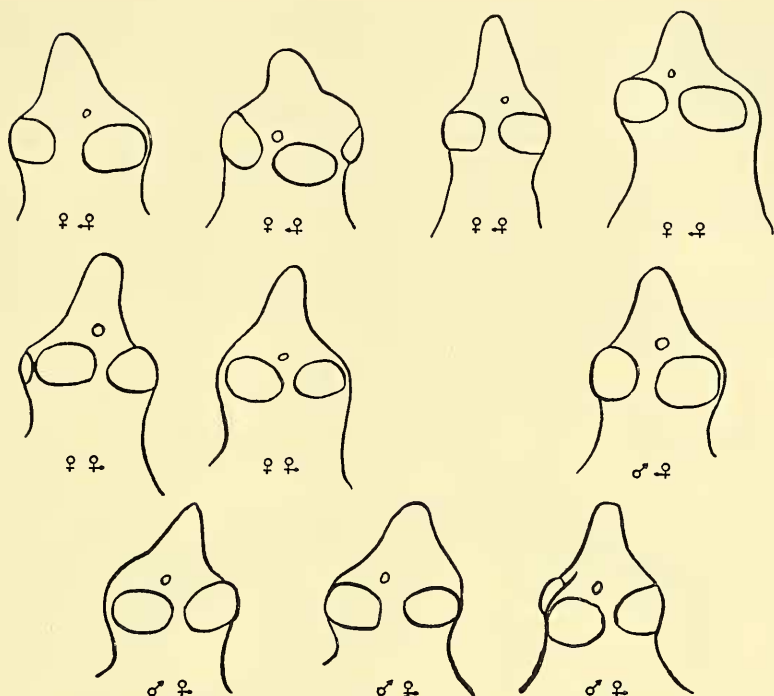
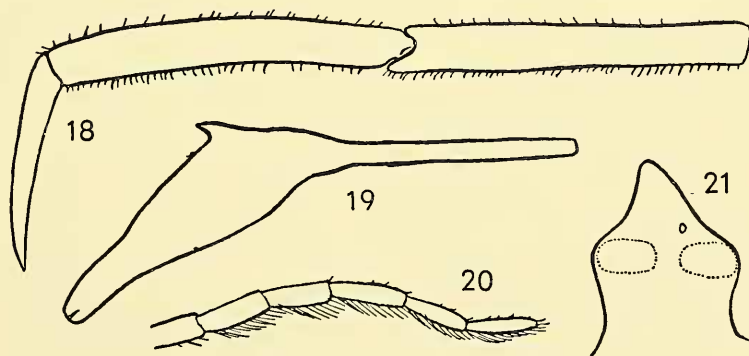


Fig. 17. *Rhopalorbhynchus lomani* spec. nov., from John Murray Exp. Stat. M.B., D. (Red Sea). Various types of eye tubercles, in side view

First leg, tarsus 1.53, 1.87; propodus 1.53, 2.07; claw 0.87, 1.00.

Third leg, femur 6.4, 7.5; tibia 1 5.6, 7.1; tibia 2 5.3, 6.7; tarsus 1.40, 1.73; propodus 1.53, 2.27; claw 0.90, 1.20.

Variability: The slenderness of the palp segments 7 to 10 varies to some extent. Also, the absolute size of adult specimens is subject to variation. The specimens



Figs. 18—21. *Rhopalorbhynchus lomani* spec. nov., male syntype of *R. gracillimus* Carpenter, from Percy Sladen Trust Exp. Stat. C 12 (Saya de Malha). 18, distal segments of first leg; 19, proboscis; 20, distal segments of palp; 21, eye tubercle from left-hand side

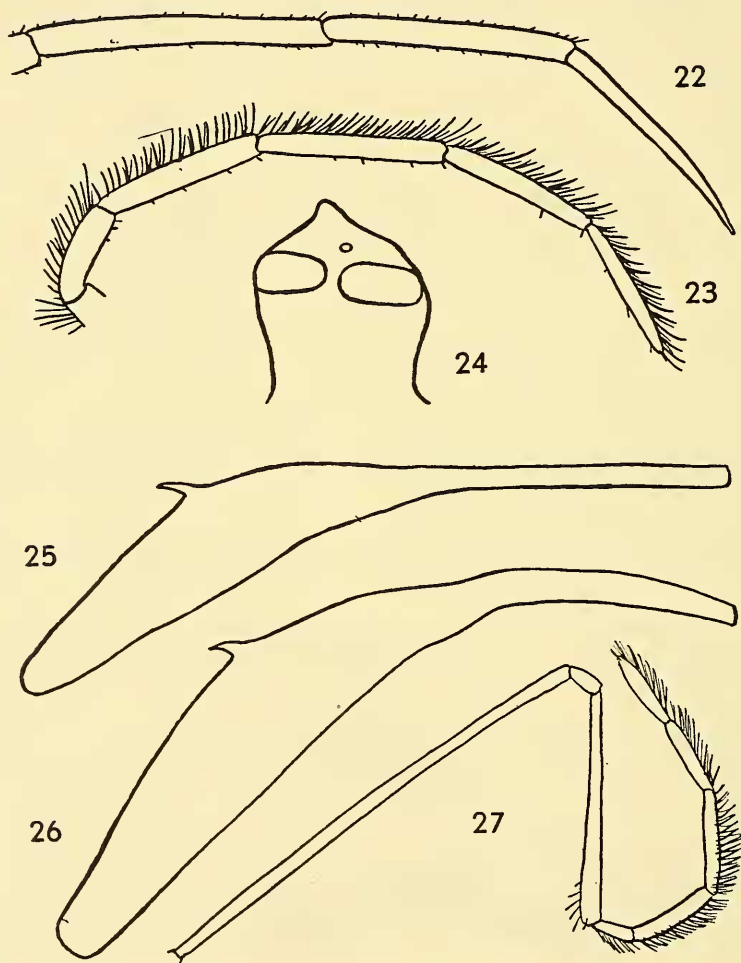
from the John Murray Expedition, for instance, are about 1.5 times as large as the male from Saya de Malha. The shape of the eye tubercle is fairly constant.

This species is named in honour of Dr. J. C. C. LOMAN (1856—1929), who has been the first to describe and figure it (under the name of *Rb. kröyeri*).

***Rhopalorhynchus sibogae* spec. nov. (Figs. 22—27)**

Rb. kröyeri, Loman, 1908 (part., only about half the number of specimens taken at Siboga Stat. 50), pl. XV fig. 217 only.

Material and types: 12 ♀, 18 ♂ (incl. 1 ♂ holotype, and 1 ♀ allotype). Siboga Stat. 50. Labuan Badjo, West coast of Flores. 27—36 m. Mud and sand. Zool. Museum Amsterdam cat. no. Pa. 1310—1311.



Figs. 22—27. *Rhopalorhynchus sibogae* spec. nov., from Siboga Stat. 50. 22, distal segments of third leg, ♂; 23, distal palp segments of ♂; 24, eye tubercle of ♂ from left-hand side; 25, proboscis of ♂; 26, proboscis of ♀; 27, palp of ♀

Distribution: Only known from the type locality.

Diagnostic characters: Proboscis resembling in outline that of *Rb. kroeyeri*. Its inflated part is sausage-shaped. The strong tooth, however, is situated distinctly before the middle of the inflated part (in six specimens on 39%, 39%, 40%, 41%, 42%, 43%). Eye tubercle, as in *kroeyeri*, lowly conical above the eyes. Palp segment 6 relatively short, from $\frac{1}{2}$ to $\frac{2}{3}$ of segment 7. Segments 7 to 10 slender. Legs longitarsal (tarsal ratio 85—99%). Claw very long, $\frac{2}{3}$ —1 times as long as the propodus. Tarsus and propodus scantily setose at the inner margin. Tarsus longer than the propodus.

Remarks: Close to *Rb. kroeyeri*, but differing in the place of the dorsal tooth on the proboscis, in the relative length of tarsus and propodus, and in the tarsal ratio.

Measurements, in mm, of specimens from Siboga Stat. 50.

Trunk, ♂ and ♀ respectively, segment 1 0.80, 1.07; segment 2 2.60, 2.67; segment 3 2.33, 2.40; segment 4 1.07, 1.13.

Width, across the 2nd lateral processes ♂ 2.00, ♀ 2.00.

Proboscis of male α 4.80, 4.47, 3.87; β 2.27, 2.20, 2.07; γ 3.87, 3.80, 3.53; δ 2.80, 2.67, 2.20; ϵ 0.93, 0.87, 0.80; 0.40, 0.40, 0.33.

Proboscis of female α 4.40, 4.47, 4.20; β 2.80, 3.07, 2.87; γ 4.67, 5.00, 4.67; δ 2.13, 2.07, 2.07; ϵ 0.97, 0.93, 1.00; ζ 0.43, 0.47, 0.47.

Femur, (male and female, respectively) P 3, 9.5, 9.9;

Tibia 1, P 3, 8.7, 8.5;

Tibia 2, P 3, 6.8, 7.3;

Tarsus, P 1, 2.53, 2.67; P 3, 2.47, 2.47; P 4, 2.40, 2.40;

Propodus, P 1, 1.93, 2.00; P 3, 2.13, 2.13; P 4, 2.27, 2.13.

Claw, P 1, 1.53, 1.53; P 3, 2.03, 1.93; P 4, 2.07, 2.03.

Rhopalorhynchus tenuissimus (Haswell)

Colossendeis tenuissima Haswell, 1885, pp. 1029—1030, pl. LVI figs. 5—8.

Rhopalorhynchus tenuissimus, Flynn, 1919, pp. 71—72, pl. XVIII figs. 1—3.

Holotype: ♂. Australian Museum, coll. no. G 5195.

Type locality: Port Denison, Queensland.

Remarks: I have not seen material of this species, and cannot judge about its status. FLYNN's opinion that it would be synonymous with *Rb. clavipes*, is certainly not correct, since *tenuissimus* is a longitarsal, and *clavipes* a brevitarsal species.

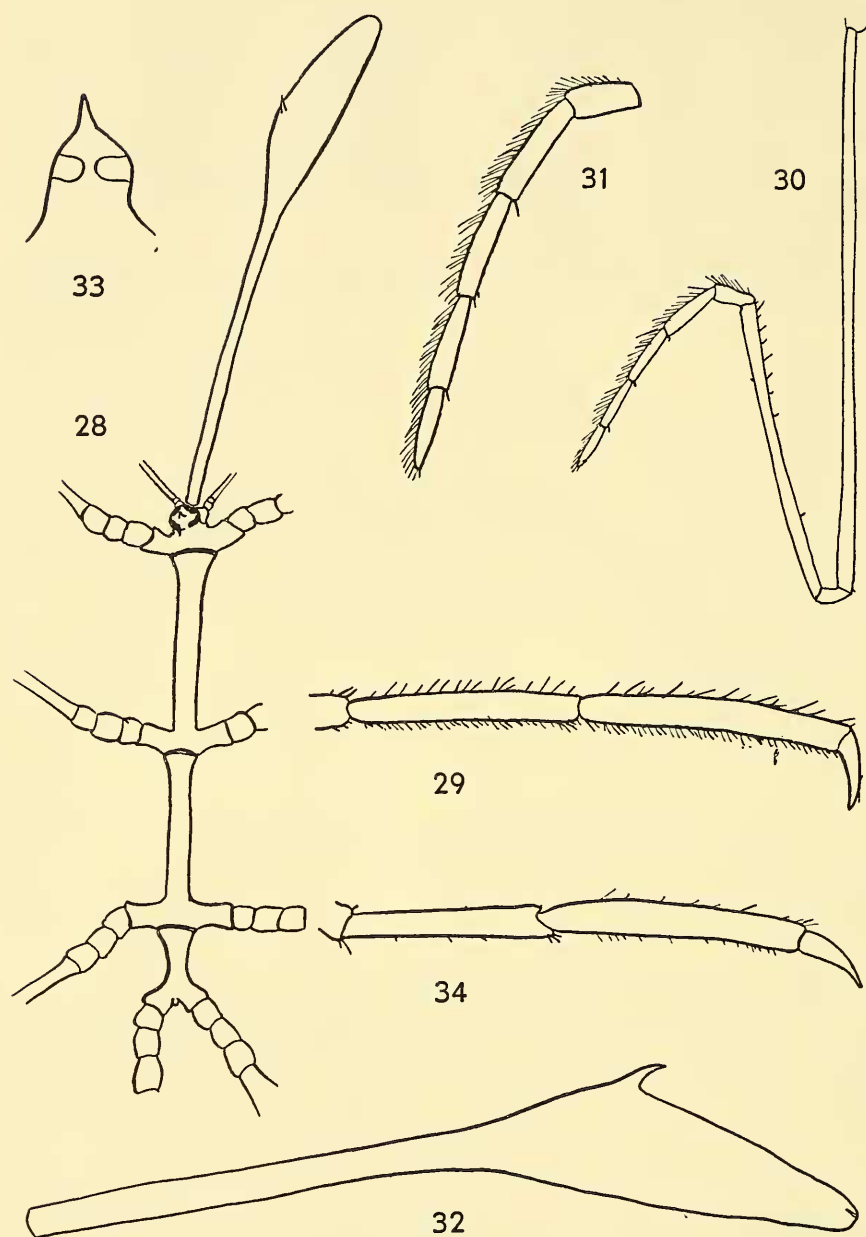
Rhopalorhynchus pedunculatum Stock (Figs. 28—34.)

Rb. pedunculatum Stock, 1957a, pp. 13—14, fig. 1.

Material and types: 1 ♂, holotype. Suez, shore. May 20, 1928. Zool. Mus. Amsterdam Pa. 1316. 1 ♂, paratype. Eylath, Israel (Gulf of Aqaba). Oct. 1951. Dept. of Zool., Hebrew Univ., Jerusalem, N.S. 197.

Distribution: Only known from these two localities in the Red Sea; littoral.

Diagnostic characters: Body extremely slender. Proboscis with a produced inflated part; tooth strong, on 39—46% of the length. Eye tubercle acutely pointed above the eyes. Palp segment 6 relatively short, $\frac{1}{2}$ — $\frac{2}{3}$ times as long as



Figs. 28—34. *Rhopalorhynchus pedunculatum* Stock, male. (28—31, from Eylath, Gulf of Aqaba; 32—34, from Suez, Red Sea). 28, dorsal view of trunk; 29, distal joints of second leg; 30, palp; 31, distal palp joints; 32, proboscis; 33, eye tubercle from the left-hand side; 34, distal joints of second leg

segment 7. Palp segments 7 to 10 not very slender. Legs brevitarsal (tarsal ratio in the two specimens examined 51% and 59%). Claw on all legs less than $1/3$ of the propodus. Tarsus and propodus setose at the inner margin, but the density of the setation is subject to variation.

Remarks: The species is characterized by the long stalk of the proboscis (longer than the inflated part), and the short claw on the legs. It is the slenderest species of the genus. The specific name alludes to the long stalk of the proboscis.

Measurements, in mm, of the male (holotype) and the male (paratype), respectively.

Trunk, segment 1, 0.40, 0.43; segment 2, 1.57, 1.53; segment 3, 1.27, 1.47; segment 4, 0.50, 0.57.

Width, across the 2nd lateral processes, 0.93, 0.80.

Proboscis α 2.67, 3.60; β 1.03, 0.97; γ 1.70, 1.80; δ 1.80, 2.67; ϵ 0.47, 0.50; ζ 0.20, 0.23.

First leg (holotype), tarsus, 0.87; propodus, 1.03; claw, 0.27.

Second leg (paratype), tarsus, 1.10; propodus, 1.20; claw, 0.33.

Third leg, femur 4.7, 5.3; tibia 1 4.3, 4.5; tibia 2 3.9, 4.9; tarsus 0.87, 1.00; propodus 1.07, 1.20; claw 0.33, 0.33.

Fourth leg, tarsus 0.87, 1.00; propodus 1.13, 1.27; claw 0.33, 0.33.

Variation: The specimen from Suez resembles in most respects that from Eylath, but has the stalk of the proboscis much shorter (Suez: $\delta/\gamma = 18/17$; Eylath: $\delta/\gamma = 27/18$), and the setation of the propodus less dense.

Rhopalorhynchus clavipes Carpenter (Figs. 35—38)

Rb. clavipes Carpenter, 1893, pp. 24—25, pl. II figs. 1—10.

Rb. kröyeri, Calman, 1923 (part.), pp. 268—270.

Material examined: 1 ♀, holotype. Dredged between reefs off Murray Island, Torres Strait. About 15 fathoms. Dec. 1888. Brit. Mus. (Nat. Hist.) 92.12.28.1. — 1 ♂, doubtfully referred to this species. Labelled: Indian Museum, no history. Brit. Mus. (Nat. Hist.) 1933.10.6.2 (this specimen has been cited by CALMAN, 1923).

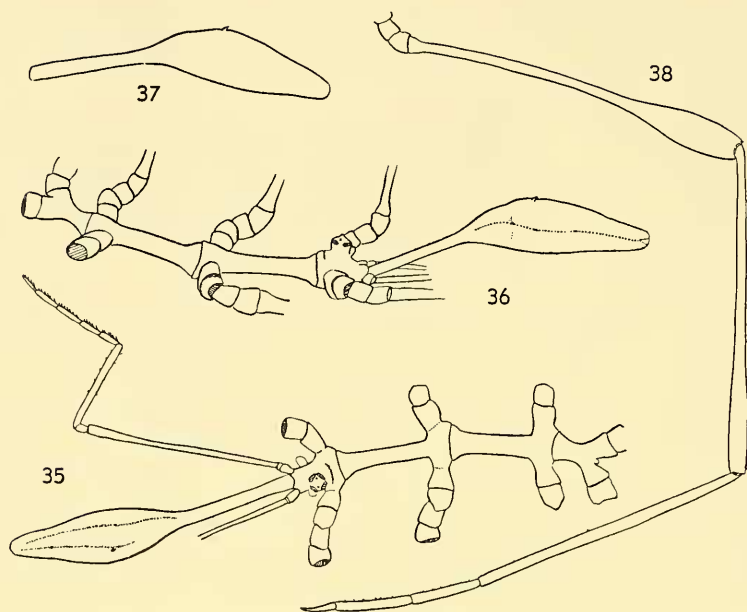
Distribution: Only known with certainty from Torres Strait.

Diagnostic characters: Proboscis with a nearly regularly club-shaped inflated part; the tooth is not very prominent, situated on 37% of the length. Eye tubercle lowly conical. Palp segment 6 rather long, $2/3$ to 1 times as long as segment 7. Segments 7 to 10 not very slender. Legs brevitarsal (tarsal ratio of 3rd leg in holotype 67%). Claw nearly half the propodus. Tarsus and propodus only provided with some scattered hairs at the inner margin.

Remarks: The Indian Museum specimen agrees with *clavipes* in the tarsal ratio (62%), the place of the tooth on the proboscis (on 36%), the length of the palp joints and the shape of the eye tubercle, but has the claw slightly longer (more than half the propodus) and the proboscis slightly more produced.

Measurements, in mm, of the female (holotype) and the male from the Indian Museum, respectively.

Trunk, segment 1, ♀ 0.80; segment 2, ♀ 1.93; segment 3, ♀ 1.87; segment 4, ♀ 0.80.



Figs. 35—38. *Rhopalorhynchus clavipes* Carpenter, female holotype, from Torres Strait. 35, dorsal view of trunk; 36, lateral view of trunk; 37, proboscis; 38, first leg

Width, across the 2nd lateral processes ♀ 1.80.

Width of trunk, without lateral processes ♀ 0.33.

Proboscis (♀, ♂, respectively) α 3.15, 3.00; β 1.85, 1.67; γ 2.93, 2.60; δ 2.07, 1.73; ϵ 0.90, 0.67; ζ —, 0.40.

First leg, ♂, tarsus, 1.07, propodus, 1.07, claw, 0.67.

Third leg, ♀ and ♂ respectively, coxa 1, 0.33, —; coxa 2, 0.33, —; coxa 3, 0.33, —; femur, 6.5, 5.7; tibia 1, 5.3, 4.9; tibia 2, 4.7, 5.1; tarsus, 1.20, 1.13; propodus, 1.40, 1.33; claw, 0.63, 0.73.

Fourth leg, ♂ tarsus, 1.07, propodus, 1.20, claw, 0.77.

Rhopalorhynchus gracillimus Carpenter (Figs. 39—56)

Rb. gracillimus Carpenter, 1907, pp. 99—100, pl. 13 figs. 25—32 (part., all records except that from Saya de Malha).

Rb. kröyeri, Loman, 1908, pp. 26—27 (part., only the specimen from Siboga Stat. 310), pl. XV fig. 218 only.

Rb. kröyeri, Calman, 1923, pp. 268—270 (part.).

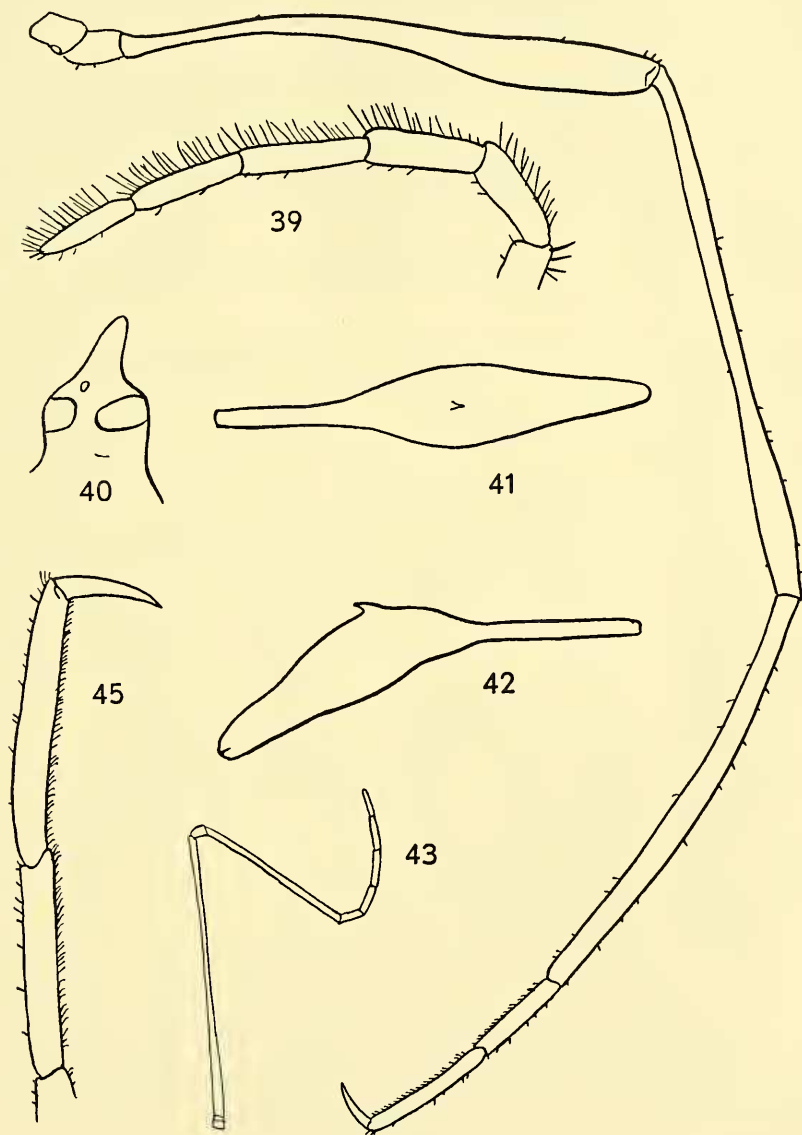
Rb. kröyeri, Barnard, 1954, pp. 88—89, fig. 2.

Material examined: 2 females. Percy Sladen Trust Exp., South Nilandu, Maldiv Islands. One of these has been selected as lectotype, Brit. Mus. (Nat. Hist.) 1908.1.6.11—15. — 1 female. Siboga Stat. 310. Sapeh Bay, Sumbawa. 73 m. Bottom: sand and corals. Zool. Mus. Amsterdam Pa. 1315. — 2 males, 1 female. Off Cape Natal, Durban (South Africa). 85 fathoms. South African Mus.

Distribution: East Indies (Sumbawa), Indian Ocean (Maldives), east coast of South Africa (BARNARD, 1954).

Bathymetrical range: 0—156 m.

Diagnostic characters: Proboscis with a narrowly produced inflated part. The tooth is situated on 18 to 27% of its length (in 4 measured specimens on 18%, 20%, 24%, and 27% respectively). Eye tubercle with a high, narrowly conical



Figs. 39—45. *Rhopalorbynchus gracillimum* Carpenter, female syntype, from the Maldivian Islands. 39, distal palp segments; 40, eye tubercle from the right-hand side; 41, proboscis in dorsal view; 42, proboscis from the left-hand side; 43, palp; 44, leg; 45, distal segments of leg.

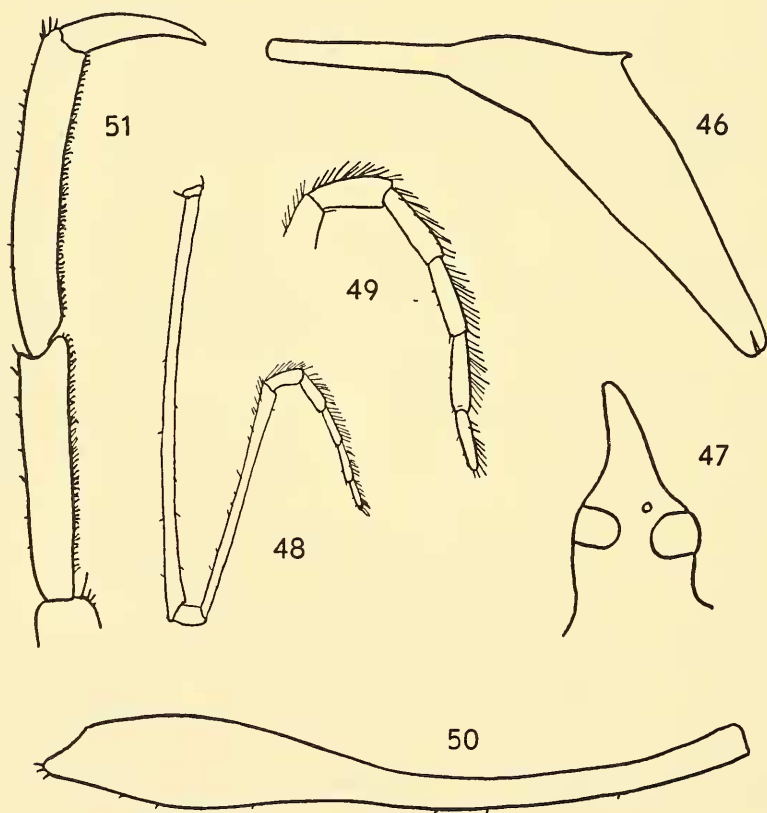
to finger-shaped apical point. Palp segment 6 relatively long, from slightly shorter to slightly longer than segment 7. Palp segments 7 to 10 short. Legs brevitarsal (tarsal ratio of 3rd leg in 4 specimens 51%, 57%, 61%, and 65%). Claw $\frac{1}{3}$ to $\frac{1}{2}$ of the propodus. Tarsus and propodus densely covered with setae at the inner margin.

Variability: The shape of the narrowed apical part of the eye tubercle varies somewhat. The tarsus is in the South African specimens very short (slightly over half the length of the propodus), in the other material only slightly shorter than the propodus. Also in other respects, the South African specimens are somewhat aberrant (finger-shaped tip of eye tubercle, long 7th palp joint, short stalk of proboscis).

Measurements of the female, lectotype (from the Maldive Islands), and of the female from Siboga Stat. 310, respectively (in mm).

Trunk, segment 1, 0.66, 0.77; segment 2, 1.27, 1.73; segment 3, 1.25, 1.57; segment 4, 0.53, 0.70.

Width across the 2nd lateral processes, 1.10, 1.40.



Figs. 46—51. *Rhopalorbynchus gracillimum* Carpenter, female from Siboga Stat. 310. 46, proboscis; 47, eye tubercle from the left-hand side; 48, palp; 49, distal palp segments; 50, femur of 4th leg; 51, distal segments of 3rd leg

Proboscis α 2.33, 3.03; β 1.80, 2.80; γ 2.47, 3.67; δ 1.40, 2.33; ϵ 0.63, 0.90; ζ 0.23, 0.33.

First leg (♀ Stat. 310), tarsus, 1.20, propodus, 1.27, claw, 0.47.

Second leg (♀ Stat. 310), tarsus, 1.13, propodus, 1.30, claw, 0.53.

Third leg (lectotype), coxa 1, 0.40, coxa 2, 0.40, coxa 3, 0.33, femur (lectotype and ♀ Stat. 310, respectively), 4.4, 6.0; tibia 1, 4.1, 5.9; tibia 2, 4.0, 5.3; tarsus, 0.80, 1.10; propodus, 1.26, 1.33; claw, 0.56, 0.53.

Fourth leg (♀ Stat. 310), tarsus, 1.03, propodus, 1.23, claw, 0.57.

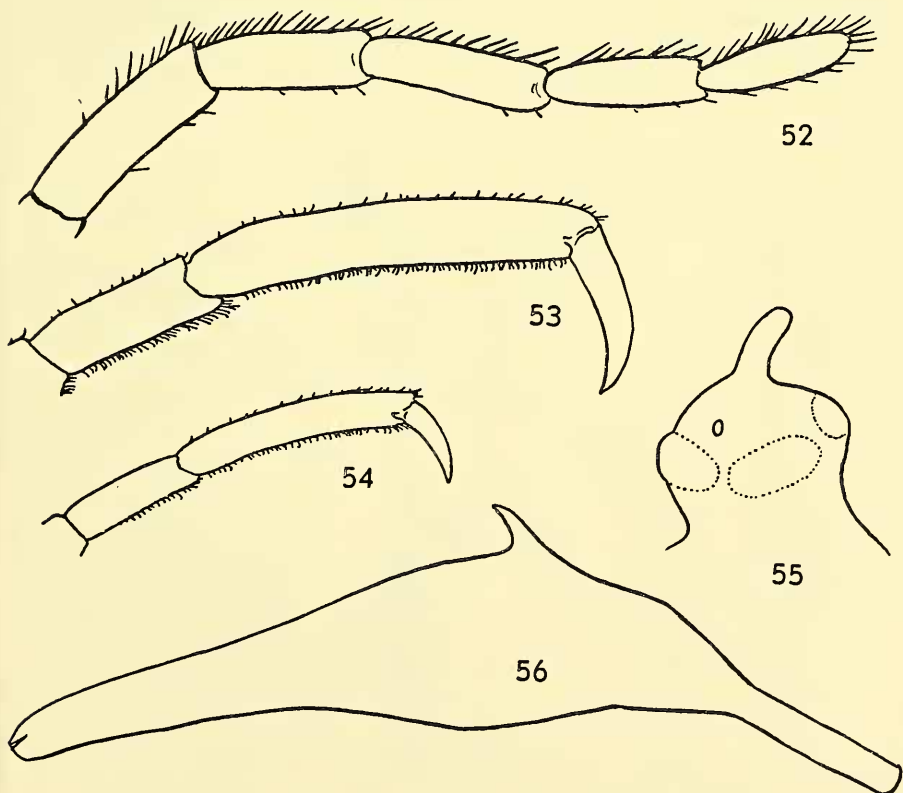
Measurements of a female and a male from South Africa, respectively.

Trunk (♂ only), segment 1, 1.00, segment 2, 1.53, segment 3, 1.33, segment 4, 0.47.

Width across the 2nd lateral processes (♂) 1.33.

Proboscis (♂ and ♀), α 3.73, 2.06; β 4.67, 2.97; γ 5.67, 3.67; δ 1.20, 1.00; ϵ 1.47, 1.07; ζ 0.47, 0.33.

First leg ♂, tarsus 1.00, propodus 1.40, claw 0.53.



Figs. 52—56. *Rbopalorbynchus gracillimum* Carpenter, from Durban, South Africa. 52, Distal segments of palp; 53, distal segments of 4th leg of ♂; 54, distal segments of leg of ♀; 55, eye tubercle of ♂ from right-hand side; 56, proboscis of ♀.

Second leg, femur 8.8, 5.5; tibia 1 8.3, 5.5; tibia 2 7.3, 4.4; tarsus 1.10, 0.80; propodus 2.00, 1.53; claw 0.60, 0.57.

Third leg ♂, tarsus 0.80, propodus 1.67, claw 0.67.

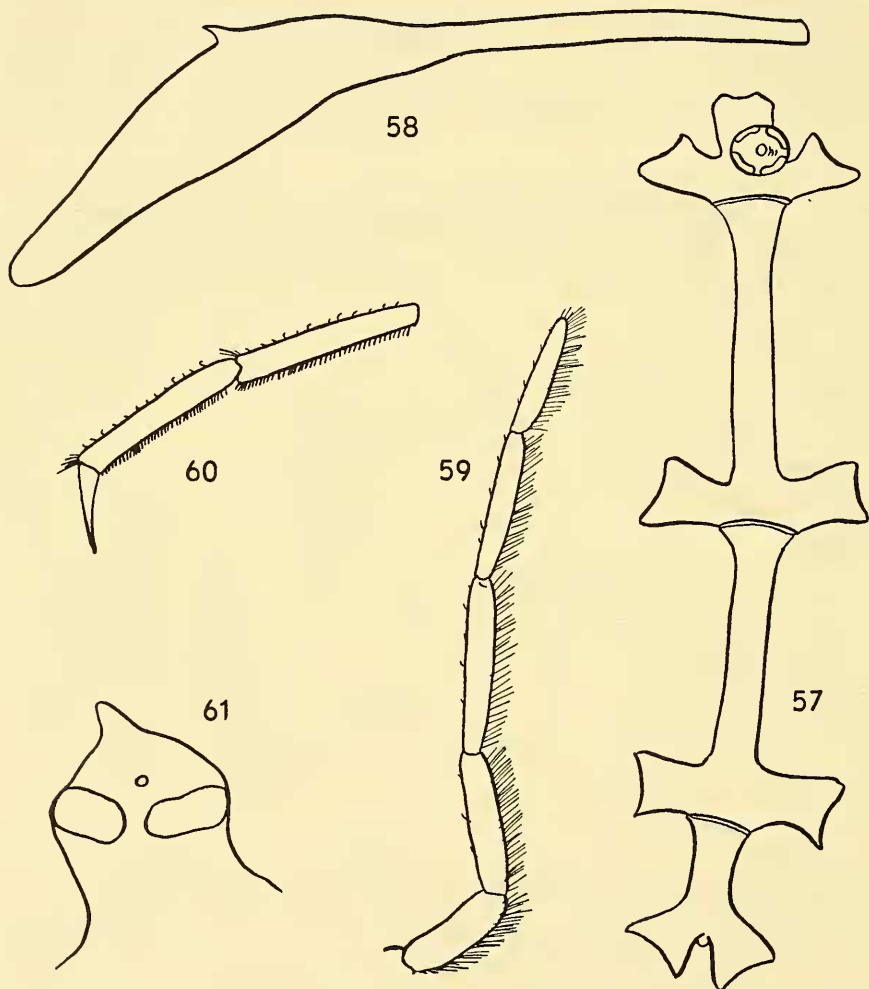
***Rhopalorhynchus mortenseni* spec. nov. (Figs. 57—61)**

Rb. kröyeri, Stock, 1954, pp. 161—162 (part., the Jolo record only).

Material and types: 1 male (holotype) and 1 female (allotype). Dr. Th. MORTENSEN's Pacific Expedition. Off Jolo, Philippine Is., about 25 fathoms. Sand and corals. March 19, 1914. Zool. Mus. Copenhagen.

Distribution: Only known from the type locality.

Diagnostic characters: Proboscis produced, but not so strongly as in *gracillimum*.



Figs. 57—61. *Rhopalorhynchus mortenseni* spec. nov., holotype and allotype, from Jolo, Philippine Is. 57, Trunk of ♂ in dorsal view; 58, proboscis of ♂; 59, distal palp segments; 60, distal joints of 1st leg of ♀; 61, eye tubercle of ♂, from the left-hand side.

The tooth is situated at 34—35% of the length of the inflated part. Eye tubercle with a narrowly conical apical point, which is, however, distinctly lower than in *gracillimum*. Palp segment 6 about $\frac{2}{3}$ of palp segment 7. Segments 7 to 10 very slender. Legs brevitarsal (tarsal ratio of 3rd leg 46%). Claw about half as long as the propodus. Tarsus and propodus with a dense setation at the inner margin.

Remarks: This species is, as to the shape of the eye tubercle and the proboscis, intermediate between *gracillimum* and *clavipes*. The setose tarsal joints agree with *gracillimum*, the place of the tooth on the proboscis with *clavipes*. *Rb. mortenseni* differs from both in the slender distal palp joints and in the tarsal ratio.

Named in honour of Dr. Th. MORTENSEN (1868—1952), who has collected this, and many other interesting pycnogonid species on his various expeditions.

Measurements, in mm, of the ♂ (holotype) and the ♀ (allotype).

Trunk, ♂, segment 1, 0.87, segment 2, 2.80, segment 3, 2.53, segment 4, 1.07. Width across the 2nd lateral processes (♂), 1.33.

Proboscis (♂ and ♀, respectively) α 4.80, 5.33; β 2.73, 3.93; γ 4.13, 6.07; δ 2.93, 2.80; ϵ 0.80, 1.10; ζ 0.33, 0.43.

First leg ♀, tarsus, 1.60, propodus, 1.40, claw, 0.73.

Third leg ♀, femur, 11.7, tibia 1, 11.0, tibia 2, 8.5, tarsus, 1.60, propodus, 1.53, claw, 0.73.

Fourth leg ♀, tarsus, 1.60, propodus, 1.53, claw, 0.77.

THE EVOLUTIONARY SIGNIFICANCE OF THE GENUS *Rhopalorbhynchus*

The species of the genus *Rhopalorbhynchus* fall quite naturally into two sections. In the one, the *kroeyeri* section, the proboscis bears a strong dorsal tooth; in the other, the *articulatum* section, such a tooth is lacking. The two sections are essentially allopartic in their distribution (fig. 62). All species of the *kroeyeri* section are tropical shallow water species. They inhabit the Indo-West-Pacific,

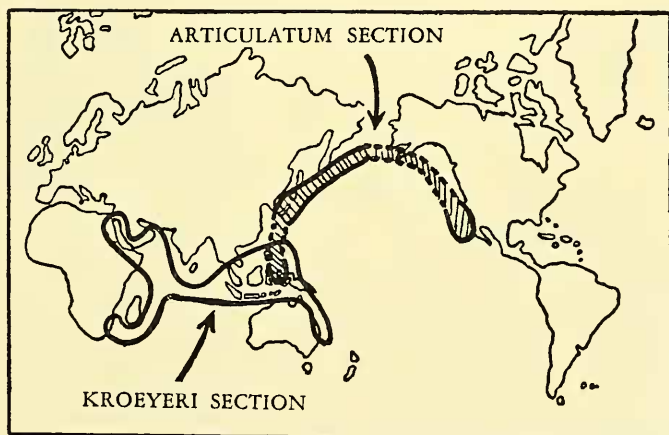
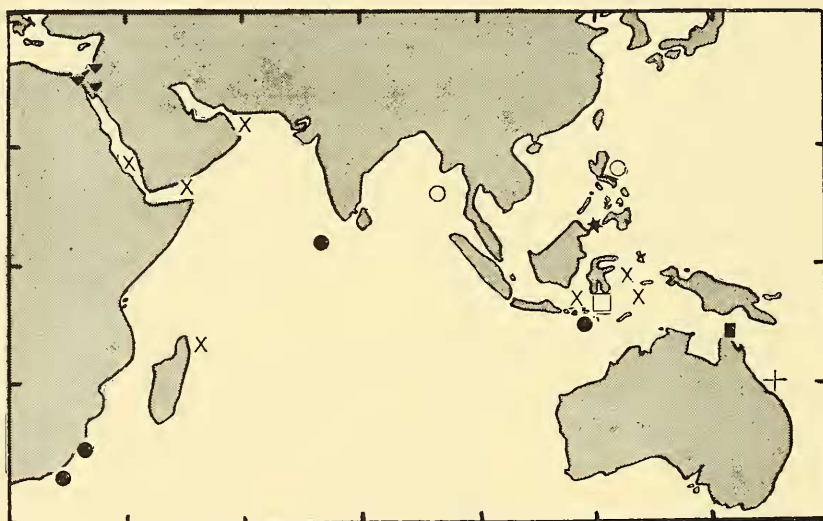


Fig. 62. The distribution of the two sections, the *kroeyeri* and the *articulatum* section of the genus *Rhopalorbhynchus*.

from South Africa and the Red Sea in the West to the Philippines and Australia in the East. The species of the *articulatum* section apparently prefer lower temperatures. They are distributed in temperate to cool waters of the northern Pacific, from Japan in the West to California in the East. One species of the *articulatum* section, *R. articulatum*, penetrates into the *kroeyeri* region, but it is noticeable that that species inhabits deep water (found in a depth of 1944 m), thus also living at low temperatures.

It is quite clear, I think, that the species of the *kroeyeri* and of the *articulatum* section represent the descendants of two originally allopatric species. These two originally allopatric species, a warm water and a cold water species, have developed through geographic speciation.

Within the *kroeyeri* section we find two species groups, the brevatarsal and the longitarsal group. Both the longitarsal and the brevatarsal species are distributed in the entire Indian Ocean and most species are sympatric in part of their range. It may be assumed that these two species groups have developed from one brevatarsal and one longitarsal species, and that these ancestral brevatarsal and longitarsal species have developed through geographic speciation. However, it must be admitted that this assumption is not substantiated by distributional or other data.



BLACKENED SYMBOLS
(BREVITARSAL GROUP)

- ▼ *pedunculatum*
- *gracillimum*
- *clavipes*
- ★ *mortenseni*

OPEN SYMBOLS
(LONGITARSAL GROUP)

- *kroeyeri*
- *sibogae*
- + *tenuissimum*
- X *lomani*

Fig. 63. The distribution of the species belonging to the *kroeyeri* section of the genus *Rhopalorhynchus*.

Within the brevitarsal and the longitarsal group there are distinct indications that the species have developed by means of geographic speciation.

In the brevitarsal group there is one central species, *R. gracillimum*, being distributed throughout the Indian Ocean from the East Indies to South Africa. In the more peripheral parts of the Indian region, viz, in the Red Sea, on the coast of North Australia and on the Philippine Islands, this central species is replaced by other species. Apparently, in these outposts of the distribution area of the brevitarsal group, geographic isolation followed by speciation was more easily realized than in the distributional centre.

The central species in the longitarsal group is *Rb. lomani*. There again, other species came to development in the periphery of the distribution area of the longitarsal group. As in the brevitarsal group, the peripheral populations on the Philippine Islands and on the northern coast of Australia developed through geographic isolation into full species.

On the whole, the distribution pattern of the species of *Rhopalorhynchus* is in good agreement with the principle of "centrifugal speciation" (BROWN, *Quart. Rev. Biol.*, 1957, vol. 32, p. 247).

That we are dealing with species, and not with subspecies, is clear at once from the distribution-pattern of the various forms of the genus *Rhopalorhynchus*. In the longitarsal group *Rb. lomani* is sympatric in part of its range with *Rb. sibogae*. Since the forms can live in each other's area without mixing, they must be considered "good" species.

In the brevitarsal group, it is true, no sympatric forms are known. But in analogy with our experience in the longitarsal group it is consistent to consider the various morphological forms in the brevitarsal group also good species.

SUMMARY OF THE INTERPRETATION OF THE SPECIATION IN *Rhopalorhynchus*

1. Two sections can be distinguished: the *articulatum* section (proboscis un-toothed) and the *kroeyeri* section (proboscis toothed). The species belonging to the *articulatum* section all are inhabitants of cooler waters and are supposed to be descendants of one ancestral cold water species. The species belonging to the *kroeyeri* section all are inhabitants of warmer waters and are supposed to be the descendants of one ancestral warm water species.

2. The ancestral cold water species and the ancestral warm water species have been developed through geographic speciation.

3. Within the *kroeyeri* section two species groups exist: the longitarsal and the brevitarsal group. These groups have been developed through geographic speciation.

4. The longitarsal group is distributed nowadays in the entire Indian region. The central species in the group is *Rb. lomani*. In the periphery of the distribution area, other species came to development through geographic speciation.

5. The brevitarsal group is distributed nowadays in the entire Indian region. The central species in the group is *Rb. gracillimum*. In the periphery of the distribution area, other species came to development through geographic speciation.

6. The distribution of the species forms additional evidence to the theory of centrifugal speciation.

ACKNOWLEDGEMENTS

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